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Certain Effects of Electrolytic Lesions in the Hypothalamus on the Mating Behavior of the Golden Hamster.

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CERTAIN EFFECTS OF ELECTROLYTIC LESIONS IN THE HYPOTHALAMUS ON THE MATING BEHAVIOR OF THE GOLDEN HAMSTER

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ABSTRACT

Bilateral electrolytic lesions were induced in the hypothalamus of 100 sexually mature female golden hamsters by the stereotaxic technique. Of twenty-two animals with symmetrically bilateral lesions located in a trigone bounded by the nuclei lateralis, ventromedialis pars lateralis, and supraopticus, 13 refused to mate and 9 tolerated mounting by normal males when paired on at least three successive occasions when vaginal smears indicative of estrus obtained. Lesions as small as 0.072 cubic millimeters were effective in inhibiting lordosis when placed in this critical area. Lesions placed asymmetrically in the two sides of the hypothalamus, or symmetrically bilateral lesions in other areas failed to inhibit psychic estrus.

INTRODUCTION

The hypothalamus occupies an area ventral to the thalamus and forms the floor and lateral wall of the third ventricle between the optic chiasma and the mammillary bodies. It has been of interest to the morphologist and neurophysiologist for a number of years. This area has been designated as one of the most important centers in the brain stem controlling the vital phenomena of the organism. Morphologic and physiologic studies of the region have been reported for a number of vertebrates from fish to man.

Of the morphologic studies of the hypothalamus of mammals, two have been of particular significance in the present investigation. Gurdjian (1927) published the result of an extensive study of the morphology of the diencephalon of the rat; and this study had been supplemented and extended by Krieg (1932) with respect to the hypothalamus of that animal. Much of the terminology of Gurdjian was retained by Krieg in the latter's description of hypothalamic nuclear patterns and fiber connections, and many of Gurdjian's interpretations were sustained. The terminology employed in the present paper is the same as that of Krieg, to whose work reference will be made throughout the present discussion.

Auer (1951) discussed the development of the hypothalamus and cell migration from the preoptic, supraoptic, infundibular, and mammillary areas of the hypothalamus of the golden hamster. From a study of fetal, young and adult brains Auer observed that during ontogenesis there is active migration of cells from a more medial origin near the third ventricle to their ultimate position. Basing her observations on the histological examination of one adult brain, Auer concluded that the hypothalamus of the adult hamster, undescribed until that time, was in many respects similar to that of other rodents including the rat. These conclusions have been sustained by the present investigation based on examination and study of more than one hundred hypothalami.

Several experiments designed to determine the role of the peripheral nerve supply to the genital organs on mating and the estrous cycle have been reported. Sweet and Thorp(1929) excised the lower sympathetic trunks from both sides of their experimental cats and noted that the cycles were prolonged in only a few of their experimental animals and prolongation of the cycle also occured in some of the controls which were sham operated. Bacq (1931) noted no important changes in the estrous cycle of the rat after removal of both abdominal sympathetic trunks, or of the superior mesenteric plexus, or of both combined. He stated that, although there is no apparent change in the mating behavior, conception, and delivery, normal milk secretion does not occur following parturition after sympathectomy. No modification of behavior attending induced estrus in the cat was noted by Bard (1935) after abdominal sympathectomy, removal of the uteri or proximal vagina either singly or in combination. Lower abdominal sympathectomy apparently has no effect on the recurrence of the estrous cycle of the cat or rat. Bard noted, however, that, after removal of the sacral cord in combination with abdominal sympathectomy, the animals allowed the males to mount but showed no trace of response to stimulation by the penis and no after reaction.

Maes (1939) obtained estrual responses in cats six hours after complete transection of the spinal cord at the level of the first cervical segment. He stated that a hypothetical sex center should be accepted with caution.

Permanent impotence in male guinea pigs was accomplished by Bacq (1931) by removal of the hypogastric nerves and inferior mesenteric ganglia. Severance of the hypogastric nerves alone resulted in erection but no ejaculation. Erection and ejaculation were elicited within 7 minutes after complete transection of the cord between T12 and L1. Root and Bard (1937) report that erection in the cat was not abolished after section of the lumbo-sacral cord, but was eliminated after complete extirpation of abdominal chains or by inferior mesenteric ganglionectomy alone.

One means of determining the function of the nuclei of the brain stem is the use of electrolytic lesions. Destruction of these inner masses without destruction of cortical areas was accomplished by Horsley and Clarke (1908) who designed and used a stereotaxic instrument in a study of the cerebellum of the cat. With this instrument precision in study of these central areas was introduced. The original model, operated on a series of rectilinear coordinates, was quite rigid and the electrodes used consisted of wires inserted into fine glass capillary tubes. In its original form, the first model of this instrument was not entirely satisfactory for critical work. The instrument was fully described and its use was explained by these authors. Modifications and use of this instrument for more efficient placement of lesions have been discussed by Ranson (1934), Harrison (1938), Clark (1940) and Waller (1944). Brown and Henry 1934) were able to produce discrete electrolytic lesions by stimulation with currents of a frequency of 3 X 10^6 cycles per second. A type of stereotaxic instrument was used to immobilize the head of the animal. They stated that accurate control over the amount of destruction could be exercised.

Other methods have been devised for placing discrete lesions in the interior of the brain and spinal cord. Warner (1929) successfully placed lesions in the hypothalamus of two guinea pigs by enucleation of the right eyeball and insertion of a needle through the optic foramen. A similar approach was used by Grunstein (1930). Application of heat extracranially produced rounded cortical lesions 2 millimeters in diameter in rats (Dennis and Bolton, 1935). Subcortical lesions without destruction to overlying tissue was impossible by this method. Hypothalamic lesions have also been produced by irritation from the pressure of mercury in the third ventricle, and by partial destruction by electrical cautery employed in combination (Krieg, 1938). Borison and Wang (1951) have been successful in placing lesions of controllable size in the medulla of the macaque monkey by implantation of gold and glass radon "seeds" into the dorsal portion of the reticular formation.

Carpenter and Whittier (1952) summarized the various methods used and concluded by actual experiment that unipolar anode lesions produced by direct current using the stereotaxic technique is the best method for producing localized subcortical lesions in experimental animals. The stereotaxic instrument used by them was a stereotaxic micromanipulator.

Identification of neural centers affecting reproductive phenomena has been approached from several aspects. The cerebral cortex has been subjected to intensive investigation. Bard (1936) found that a female cat in which all of the neocortex had been removed entered spontaneously into estrus on two occasions during the twenty-eight months of survival. After three additional cases had occured he concluded that feline estrual behavior is not dependent upon the cerebral cortex. Pseudopregnancy has been elicited in rats following bilateral ablation of the neocortex

(Davis, 1939). The duration of this condition was the same as in normal females, but the phenomenon was more difficult to induce. Estrous cycles, mating, pregnancy, and delivery were not interrupted, although maternal behavior seemed to have been lost. Stone (1938) destroyed the neocortex of rats by electro-cautery and concluded that lesions involving approximately 40% of the cortex or more are much more disruptive of maternal behavior than of breeding, placentation, gestation, and parturition. That sense organs played little role in inducing mating activity of the rabbit was established by Brooks (1937). Destruction of the olfactory, visual and auditory senses had no effect on the sexual activity of either males or females; and the behavior of animals deprived of all three senses was likewise not affected. Ablation of the olfactory bulbs and of the neocortex as well abolished mating in both sexes. Removal of the entire forebrain, diencephalon, mesencephalic tectum, cerebellum and the anterior edge of the mesencephalic tegmentum did not affect the ejaculatory response of male _Rana pipiens_, although invasions of the posterior tegmentum resulted in complete loss of these reflexes (Aronson and Noble, 1942). However, destruction of the preoptic area of the forebrain resulted in the failure of the male to clasp the female whereas destruction of the forebrain except the preoptic area resulted in no observable changes in the mating pattern.

The findings of Beach (1940) are in disagreement with those of other authors with reference to the importance of the cerebral cortex in mating behavior. By electro-cautery he destroyed varying amounts of the cortex in sexually mature male rats. Removal of less than 20 per cent of the neocortex did not abolish copulatory behavior; but removal of 20 to 75 per cent resulted in non-copulation in males. He stated that the percentage of the non-copulators was directly proportional to the size of the lesions.

Direct stimulation or destruction of the hypothalamic area or parts thereof has resulted in alterations in the normal mating pattern of various animals. Using bipolar electrodes inserted 5 millimeters below the thalamus Haterius and Derbyshire (1937) were able to induce ovulation and to evoke slowly developing flexion of the hind limbs and pelvis of the cat. Although areas stimulated were not defined in this report, it appears that the stimulated area was quite large. These authors attributed the response to stimulation of an area directly above and anterior to the optic chiasma. Brookhart, Dey and Ranson (1940), using ovariectomized guinea pigs injected with preoperative doses of estrogen and progesterone, placed lesions at the level of the posterior border of the optic chiasma. All animals failed to exhibit proestrous and estrous behavior. The same results were obtained when double and quadruple doses of hormones were administered to a smaller group of experimental animals. These authors interpreted the absence of estrous behavior not as a result of the lack of ovarian hormones, but rather as a result of the destruction of the part of the central nervous system responsible for complex behavioral patterns. Lesions placed in the hypothalamus of the guinea pig before mating and during pregnancy were reported by Dey, Fisher, Berry and Ranson (1940). Large lesions were placed in the ventral area of the hypothalamus between the optic chiasma and the pituitary stalk. Despite the fact that only 23 per cent of the females became pregnant after mating while the remaining 77 per cent became sterile, normal cycles were maintained by these animals (indicating no interruption of pituitary function). Dey (1941) divided his postoperative guinea pigs with hypothalamic lesions into three groups as determined by the condition of the vaginal membrane. He noted that one group remained cyclic, whereas others presented permanently open or closed vaginal membranes. In the group showing no change in the cyclic nature of the vaginal smears he noted that the lesions placed in the hypothalamus were widely scattered and differed in size. The lesions were always rostral to the mammillary bodies and within the substance of the hypothalamus. In those animals in which the vaginal membranes were permanently open the lesions were stated as being located between the optic chiasma and the median eminence. The third group exhibiting permanently closed membranes had lesions in the hypothalamus from the rostral end of the median eminence to the premammillary complex.

The Horsley-Clarke stereotaxic instrument was used by Brookhart, Dey and Ranson (1941) to place lesions in the anterior hypothalamus of guinea pigs to determine the effect of such destruction on the mating behavior of these animals. After a current of 3 milliamps had been employed for 30 seconds mating was abolished. The size of the lesions induced by these authors was not stated but it is assumed that they were of considerable size. They stated that the central mechanisms for estrual behavior must be located somewhere in the preoptic or septal areas. To test the efficacy of lesions in the hypothalamus of male guinea pigs in abolishing sexual excitement Brookhart and Dey (1941) placed lesions with the use of unipolar electrodes and the Horsley-Clarke instrument. They used the presence or absence of pregnancy in a female paired with the postoperative male as the criterion in ascertaining mating activity of the males. Since motile sperm and evidence of spermatogenesis were found, these authors concluded that no gonadotrophic center had been affected. Two of the nine males exhibited normal sexual behavior while but three pregnancies were reported from pairings of the other seven animals. While the results demonstrated here are not profound, they indicate that the males with lesions in the ventral hypothalamus between the optic chiasma and the pituitary stalk present reduced or absent sexual activity. Using the Horsley-Clarke stereotaxic instrument without success, Clark (1942) placed lesions with a small dental spatula and found that copulatory behavior was absent in several male rats with lesions near the midline adjacent to the third ventricle. Bard (1940), in a good review of the literature to that date, reported a paper by Ranson (1934) in which the latter author stated that cats with large lesions in the tuber cinereum, and lateral to and behind the infundibulum mated, gave birth to full-sized litters and nursed and cared for their young. Bard also reported unfinished research which he and Dr. H. W. Magoun had undertaken. Only a few cases were reported and the writer was unable to find reference to any published article in the literature. Relatively gross lesions as evidenced by serial photographs of the hypothalamus taken at 1 millimeter intervals prevented estrual behavior. Lesions of large size are of little value in attempting to localize specific areas responsible for mating phenomena.

The cyclic nature of the reproductive phenomena in female guinea pigs is, according to Dey (1943), under the control of the median eminence. Acyclic conditions resulted following destruction of the median eminence with three lesions in the same animal. Animals with lesions slightly rostral or caudal to the median eminence or destruction of only a small area of the eminence had no effect on the cyclic phenomena, mating, or conception. Large lesions in the anterior hypothalamus of the female guinea pig resulted in a condition of constant estrus (Dey, 1943). Attempts to induce ovulation in these animals by injection of copper acetate into the jugular vein, third ventricle and pituitary were without success.

A possible facilitative effect of progesterone on the brain stem was suggested by the experiments of Kent and Liberman (1949). Following injection of progesterone into the lateral brain ventricle of ovariectomized golden hamsters in amounts much too small to induce mating by the subcutaneous route, animals mated within one hour or less, and in five out of six trials they mated within ten minutes. These authors concluded that progesterone may affect one or more brain centers causing the female to enter the physiologic and psychologic state known as psychic estrus. The findings of these authors was the stimulus for the present study, the purpose of which has been to locate an area in the hypothalamus which, when destroyed by small bilaterally symmetrical electrolytic lesions, will reduce or abolish the mating responses of the female hamster.

MATERIALS AND METHODS

One hundred female golden hamsters weighing from 78 to 116 grams were used in the present investigation. These animals were of the L.S.U. strain maintained by the Department of Zoology, Physiology and Entomology at Louisiana State University. Of these, eighty-six were virgin females 73 to 222 days of age at the time of placement of the lesions; nine were primiparous or multiparous females of uncertain age; and five were normal cyclic animals of unknown history. All animals were sexually mature and had exhibited at least three consecutive estrous cycles prior to placement of the lesions.

The weight of each animal to the nearest 0.5 gram was recorded daily from the first day the animals were segregated until the completion of the experiment. For convenience, weighing preceded the making of vaginal smears.

After an animal was segregated for the experiment, vaginal smears were made for twelve days thereafter, or until three estrous smears were recorded to determine whether or not a cyclic condition obtained. At the time that the animal presented a vaginal smear indicative of estrus, a male was placed in the cage and the time required for the female to exhibit lordosis was recorded so that comparisons could later be made with the mating response of this animal after lesions were placed. In 67 cases the females were allowed to mate with a vasectomized male[1] at the fourth estrus. It was not known whether the exhibition of lordosis

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[1]Operation for vasectomy was by double ligation of the vasa deferentia and transection between the ligatures.

alone could be used as a criterion for establishment of willingness to mate. In all later cases exhibition of lordosis alone was considered as indicative of willingness to mate.

Following termination of pseudopregnancy in those animals allowed to mate with a sterile male, vaginal smears were made for twelve days or until three estrous smears had been observed to determine whether or not the female had returned to a cyclic condition.

Modification of the Horsley-Clarke Stereotaxic Instrument

The Horsley-Clarke stereotaxic instrument originally designed for use on the cat was used in the present investigation. In this study ear bars designed for the cat were used, although the ear plugs formerly used were dispensed with. The two clamps designed for the parietal region of the skull of the cat and those designed for beneath the orbits of the cat were replaced by an upper head plate and lower head plate respectively (Figure 2).

The upper and lower head plates were constructed from sheets of aluminum alloy 2 millimeters thick. Before a pattern was made, from which to copy the final modifications, the points of attachment to the instrument of the parietal and orbital bars for the cat were separated as far laterad as possible.

The upper head plate consisted of a ring 6 millimeters wide with an inside diameter of 17 millimeters. The diagonal supports were attached to the instrument by two cap screws inserted through two holes (Figure 2A, A and A') and into those provided on the instrument for attachment of the parietal bars. The distance between these holes was 42 millimeters. There was no movement of this plate in a lateral direction.

The lower head plate (Figure 2B) consisted of a 26 X 26 millimeter square plate. The diagonal supports of this plate were attached to the instrument by two vertical columns (Figure 2C, B and B') 4 millimeters in diameter. These columns, 53.5 millimeters apart, were fitted snugly but easily into the holes provided on the instrument for attachment of the orbital bars (for use on the cat). As in the case of the upper head plate, no lateral movement of this plate was observed.

To prevent pressure on the larynx a small portion (Figure 2B, X), 7 X 9 millimeters was removed from the rear edge of the lower head plate.

The lower electrode carrier which was originally used on the instrument gave satisfactory results when, as in most cases, the 22 gauge electrode was used; but when the 28 gauge electrode was used, as in some of the cases, there existed a large area through which the smaller wire could be moved in any direction. By using a small sleeve of glass tubing 9 millimeters long the diameter was reduced to that which just enabled the smaller electrode to pass through. This sleeve was obtained by heating a portion of larger diameter soft glass tubing and pulling the ends apart. The ends of the sleeve were burnished to prevent possible displacement of the insulating material on the electrodes as the latter were raised and lowered. This sleeve was securely fitted into position on the lower electrode carrier by gentle tapping.

Preparation of Electrodes

Unipolar electrodes used in the present investigation were constructed of nichrome[2] wire B&S gauge 22 and 28. Approximately thirty-

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[2]Driver-Harris Company, Harrison, New Jersey

six inch segments of the wire were taken from the spool and straightened by traction. With wire of this length, an increase in length of approximately one-half inch was sufficient to render the wire straight with no appreciable loss of tensile strength. All electrodes penetrated the dura mater without bending.

Following straightening, the wire was cut into 22 centimeter lengths. One end of the wire was sharpened under a binocular dissecting microscope, using a dental drill with an emery wheel attachment. The electrodes were then dipped into a narrow tube containing polystyrene coil dope and were then inserted into a large cork and allowed to dry. (The fine wire enamel with a china-wood oil base used by Ranson (1934) was not available.) Although the insulating plastic used in the present study was satisfactory, subsequent investigation will be made with a different material. When the electrodes were dry (after 48 hours) a second coat was applied in the same manner. Completed electrodes were stored in a wooden thermometer case to protect them from dust and bending.

Final preparation of the electrodes involved removal of the insulating material from the sharpened tips. This was accomplished with the aid of a binocular dissecting microscope, a dental drill, and an emery wheel attachment. In the case of the 22 gauge electrodes, approximately three-fourths millimeter of the tip was exposed; in the case of the 28 gauge electrodes, approximately one-half millimeter was exposed.

Operation of Animals and Placement of Lesions

Immediately preceding operation the animals were weighed to the nearest 0.5 gram. During previous experiments, the author had found that the average dosage of Nembutal[3] required to anaesthetize these animals was 80-100 milligrams/kilogram body weight intraperitoneally administered. This is in agreement with the findings of Orland and Orland (1946) who stated that 80 mg/kg body weight was the average dosage required to anaesthetize for one hour.

After the animals were immobilized, the hair from the dorsal portion of the head was removed with scissors. This area included all of the dorsal region of the head between the eyes from a line one centimeter anterior to the cephalic edge of the palpebral fissure to one centimeter posterior to the ears. All of the longer hairs around the ears were removed.

An incision was made in the midline dorsally from the level of the cephalic edge of the palpebral fissure caudad for 15 millimeters. Removal of the exposed galea aponeurotica was accomplished by scraping with a sharp scalpel. Any remnant of the aponeurosis remaining on the skull at the site of trepination resulted in engagement of the dental burrs.

Following this operation, the animals were adjusted in the instrument so that the exposed skull surface was centered against the upper head plate. The head was pressed against this plate, making it possible to easily insert the ear bars snugly into the external auditory meatuses. Although it is not necessary to record the readings of the coordinates on the ear bars, it is essential that the readings on either side be equal to insure exact central placement of the head in the instrument. The lower head plate was then raised into position. The function of

[3] Sodium pentobarbital

the upper and lower head plates was to prevent dorso-ventral movements of the head pivoted on the ear bars. With all these adjustments made and tightened, the electrode carrier was moved to the mid-sagittal plane, and if the animal has been properly placed in the instrument, the electrode when lowered will come to lie directly above the sagittal suture. If this alignment does not obtain, the animal should be removed from the instrument and the procedure begun again.

When the animal was properly oriented in the instrument the electrode carrier was moved to the desired point (one-half or one millimeter to the right or left of the midline) and the electrode was lowered to within one millimeter of the skull. The location of the projected trephine as indicated by the tip of the electrode was marked with an indelible pencil. This procedure was repeated on the opposite side. The animal was then removed from the instrument and bilateral trepination of the skull at previously marked sites was accomplished utilizing the dental drill and #6 and #7 dental burrs. Only the bone was pierced leaving the dura mater and periosteum of the calvarium intact.

All trephines were placed in the antero-medial area of the parietal bone at the angle formed by the coronal and sagittal sutures. No trephines could be placed less than one-half millimeter from the sagittal suture since rupture of the sagittal sinus by the dental burr invariably resulted when attempts were made to destroy areas immediately surrounding the third ventricle.

Customarily, bilateral trepination is accomplished with the animal fixed in the instrument. The small size of the hamster coupled with the greatly reduced working space inside the ring of the upper head plate made this procedure impracticable. Exact replacement of the animal in the instrument was easily accomplished.

After the animal was replaced in the instrument the indifferent electrode (cathode) was placed in the anus. It was found that this region gave the most constant resistance, and variable rheostats were dispensed with since the animal's body gave sufficient resistance to reduce the current to the desired amperage. Six one and one-half volt dry cell batteries were assembled in series and connected to the instrument via a milliammeter and a switch.

By manipulation of worm screws the electrode carrier was brought into position and the electrode was lowered to the floor of the skull. When slight bending of the wire was noted, the electrode was withdrawn until the wire assumed its straight condition. Utilization of the coordinates governing the dorso-ventral placement of the tip of the electrode allowed accurate placement of the lesions at any desired distance above the floor of the braincase. Following electrolysis, the electrode was withdrawn and a lesion was placed on the opposite side at the same location. This procedure was followed with each new animal to avoid error introduced by possible differences in skull size.

Current used in the present investigation was 1 to 4 milliamps for 1 second. Longer continuous exposure to current caused undesirable secondary burning up the course of the electrode. If more extensive burning at the tip of the electrode was desired, a series of as many as four one-second exposures was employed. Following bilateral placement of lesions, the animal was removed from the instrument and prepared for suturing.

The exposed surface of the skull was wiped with 70 per cent ethyl alcohol and sulfadiazine was applied to the periphery of the wound and to the galea. Sutures were not more than 2 millimeters apart. It was noted that by the fifth day all sutures had been removed by the animal. No cases of infection were noted.

Following placement of lesions and before the animal was returned to its cage, the cage was cleaned and sterilized. This was accomplished by scrubbing with hot water and soap followed by immersion in 2 per cent Cresylone[4]. Animals were observed during the recuperation phase for any abnormal reactions which might be correlated with the areas involved in the destruction.

Vaginal smears of the animals were examined during at least three successive estrous cycles following placement of lesions to determine whether or not any alteration in cyclic activity had occured. Each time a vaginal smear indicative of estrus was obtained a male was placed in the cage and the length of time required by those animals that accepted the male to exhibit lordosis was noted and recorded. If the animal refused to mate or fought the male, the procedure was repeated hourly until vaginal estrus no longer was indicated by smears.

Most animals were killed on the day following the third or fourth or, in some cases, the fifth pairing. Death was effected by suffocation with ether or by intrapleural injection of Nembutal. In the latter case, death was almost immediate.

Preparation of Brains for Histological Study

The brain was removed from the animals in the following manner. A mid-dorsal incision was made from the end of the snout to the level of the first cervical vertebra. The two cut edges were deflected laterad and

[4]A saponified cresylic acid solution distributed by Parke, Davis and Company, Detroit, Michigan.

ventrad. This procedure usually removed the eyes from the orbits allowing easy transection of the optic nerves, and loosened the temporalis muscle from its origin in the temporal fossa. The origins of the temporalis and masseter muscles were severed with a sharp scalpel. The snout was removed by transecting at the level of the nasal bones with heavy scissors. The skull was reflected caudad to the first cervical nerve and ventrad to the base of the orbits. Following removal, the brain was fixed in 10 per cent formalin for three days.

After preliminary fixation of the brain in toto it was trimmed in the following manner. A section was made in a transverse plane about 3 millimeters anterior to the optic chiasma. A second cross section was made at the level of the inferior colliculi and passing ventrad through the pons. Parallel sections in a sagittal plane were made from the ventral surface across the hippocampal gyri. The final trimming involved a frontal section at the level of the anterior commissure. When the dorsal portion of the brain was removed, the habenulae were clearly visible. By this procedure the area of the brain for sectioning and histological examination was limited to the hypothalamus and a small amount of surrounding tissue. This trimmed portion was then replaced in fresh 10 per cent formalin for four days.

The brains were washed in running tap water for one hour, dehydrated in alcohol, cleared in xylol, and embedded in Fisher's tissuemat (melting point 54-56^{o}C). Syracuse watchglasses pretreated with glycerin served as embedding dishes.

The brain from each animal was sectioned at 10 microns and every fifth section was affixed to a slide. An alternate series of brain sections was made. One series was stained with toluidin blue, differentiated in 95 per cent ethyl alcohol, dehydrated, cleared, and mounted in clarite. The other series was stained with Morgan's modification of Heidenhain's iron haematoxylin (Morgan, 1926). No counterstain was used with either series.

RESULTS OF ELECTROLYTIC DESTRUCTION

Mating Responses

On the basis of the nature of mating response of the animals subsequent to placing of lesions they may be grouped into four categories:

Group I: Thirteen animals refused to mate or fought the male whenever paired. This response obtained even when a vaginal smear indicative of estrus was exhibited.

Group II: Nine animals permitted mounting by the male at each vaginal estrus. Lordosis was exhibited only when the male had mounted; and the female had to be stimulated by the male before another mount was permitted.

Group III: Twenty-two animals fought the male or refused to allow mounting during the first, or first and second post-operative estrus, but exhibited lordosis and mated on estrual pairing thereafter.

Group IV: Fifty-five animals accepted the males from the first post-operative exhibition of estrus. In some animals in this group lordosis was exhibited within twelve hours after the lesions were placed.

Location of Lesions

Of the one hundred animals used in the present investigation, one died as a result of the operation. Fifty-eight animals are included in the cartograph; the remaining forty-one are entered in Table 1.

Figure 1 presents in cartographic form the location of the lesions with reference to the nuclei involved partially or wholly in the destruction. The four groups were established on the basis of mating responses following placement of lesions (see above). The figure does not include all experimental animals in Groups III and IV, selection having been made on the basis of diversity of location of the lesions, all of which failed to inhibit the mating response.

Group I: In all cases in which the mating response of the female was abolished there was bilateral involvement of the cells of the nucleus lateralis (Lat.). In all but one of the 13 animals (animal 130) there was bilateral involvement of the nucleus ventromedialis pars lateralis (V.M.L.). These two areas (Lat. and V.M.L.) appear to be the only ones that can be consistently implicated since other nuclei were involved inconsistently or unilaterally only. The lesions occured in a trigone formed by these nuclei: Nucleus lateralis (Lat.), nucleus ventromedialis pars lateralis (V.M.L.), and nucleus supraopticus (Sup.).

Group II: The same two nuclei were consistently involved in the nine animals of this group as in many animals in Group I. Two animals showed only unilateral destruction of cells of the nucleus ventromedialis pars lateralis. The same trigone was consistently involved among these animals as in the animals of Group I. The nuclei of the trigone are: nucleus lateralis, nucleus ventromedialis pars lateralis, and nucleus supraopticus with little or no involvement of the latter.

Group III: No areas except the nucleus lateralis have been consistently involved. This is the largest nucleus of the hypothalamus of this animal. Reference to Figure 1 indicating the specific nuclei involved, and to the photographs of these nuclei (Figures 3-8) indicates that the lesions in this group were quite scattered from the rostral (Figure 12) to the caudal (Figure 13) boundaries of the hypothalamus.

Group IV: Many of the lesions in these animals were located in the anterior part of, or anterior to, the hypothalamic area (compare

Figures 4 and 12). The location of the lesions of the last three animals presented in Figure 1 (168, 169, 178) is typical of many of the animals in this group (i.e. the 2 important nuclei were included only occasionally). (The figure represents only 18 of the 55 animals in this group; the remaining 37 animals are presented in Table 1)

In general, lesions placed in non-homologous areas of the two sides of the hypothalamus (Figure 11) (i.e. asymmetrical lesions) resulted in uniformly positive mating reactions. Nineteen such cases occured. These animals accepted the males and mated with the same alacrity as before the lesions were placed. Clark (1942) stated that unilateral lesions in the anterior hypothalamus failed to abolish the sexual behavior of male rats. No attempt was made to place lesions in one side only since the findings of previous authors seemed to definitely indicate the inefficacy of such procedures.

It was almost impossible to destroy completely all of the cellular components of any single nucleus without ablating at least parts of adjacent nuclei. In all cases, attempts were made to restrict the destruction. Because of the aim to be restricted, subtotal destruction of many of the nuclei resulted. In the case of some of the smaller nuclei complete ablation of the cells was accomplished. Figure 1 and Table 1 are not intended to suggest complete destruction of all nuclei listed but rather that some part of the nucleus was involved. The following nuclei were not bilaterally involved in any of the animals: nucleus filiformis parvocellularis (Fil.P.), nucleus periventricularis, anterior division (P.A.), nucleus mammillaris posterior (M.P.), nucleus hypothalamicus posterior (Post.), and the nucleus supramammillaris (Sum.). The nuclei mammillaris posterior and supramammillaris were not involved in any of the lesions.

The rostro-caudal dimension of the lesions could not be calculated more accurately than within 50 microns since every fifth 10-micron section was affixed to a slide. The other two dimensions were calculated with the use of an ocular micrometer. The volume destroyed by single lesions ranged from 0.004 cubic millimeters to 3.60 cubic millimeters. No correlation could be made between the size of the lesion and the mating response.

The range in size of individual lesions in each of the four groups was as follows: In the thirteen cases in which the animals fought or refused to allow the male to mount despite an estrous smear (Group I) the volume of the lesions ranged from 0.072 to 2.50 cubic millimeters with an average volume of destruction equal to 0.653 cubic millimeters. In the nine animals in which mating was tolerated without normal lordosis (Group II) the volume of the lesions ranged from 0.081 to 1.316 cubic millimeters with an average volume of 0.451 cubic millimeters. In Group III which included those animals which exhibited negative mating responses for the first or first and second pairings the range was from 0.019 to 3.60 cubic millimeters, the average being 0.403 cubic millimeters. In Group IV (those animals which mated or exhibited lordosis from the first estrus) the volume of destruction ranged from 0.004 to 1.449 cubic millimeters. Here the average destroyed volume was 0.200.

Following placement of lesions, twelve animals remained acyclic for lengths of time varying from 4 to 14 days. Some of these acyclic animals presented an extended diestrous smear, while others remained in constant estrus. During the acyclic condition, the animals refused to mate. All but one of these animals (#118) finally returned to a normal cyclic condition. Three of these animals persisted in refusing to mate, and were placed in Group I; two were finally placed in Group II; and seven are included in Group III.

ANCILLARY OBSERVATIONS

Pseudopregnancy

Pseudopregnancy was induced in these animals in ascertaining their willingness to mate before lesions were placed. Actual mating with a sterile male was allowed in the first 67 animals; lordosis was used as the criterios for willingness to mate in the remaining 33 animals. In some of the former cases, mating with a sterile buck was allowed on more than one occasion.

An extended diestrous interval resulted from these matings in 97.4 per cent of the trials. This is in agreement with the findings of White (1949) who reported 96 per cent in 25 trials and of Deanesly (1938) who reported 100 per cent in 22 attempts. To determine the duration of this condition, at least two criteria can be used. In an earlier paper (White, 1949), the nature of the vaginal smear was the criterion. The sudden influx of leucocytes and epithelial cells (early diestrus, Kent and Smith, 1945) was considered as indicative of an earlier termination of the condition. Using vaginal smears concomitant with the exhibition of lordosis or, if lordosis did not obtain, using early diestrus the following day as the criterion for determining the termination of the condition, the duration of pseudopregnancy was found to be from 7 to 10 days (one animal exhibiting a 7 day cycle; fifteen an 8 day cycle; sixty-two a 9 day cycle; and one a 10 day cycle). Using as the criterion the exhibition of lordosis following one or more days in which pairings resulted in refusal by the female the duration of the condition was found to be from 7 to 9 days (one exhibiting a 7 day cycle; fifteen an 8 day cycle;

and forty-nine a 9 day cycle). In these latter cases, only those animals which refused to accept the male the day preceding the exhibition of lordosis are included. This accounts for the difference in the number of cases reported. It is not known what the mating responses of the other females might have been if extensive pairings had been attempted. Willingness to mate, and not manifestation of pseudopregnancy, was of focal interest in the present investigation and extensive pairings were not attempted.

Similarity of Hypothalamic Nuclei in the Rat and Hamster

Using the descriptions and figures presented by Krieg (1932) it was possible to make direct comparisons between the nuclear patterns of the rat and golden hamster. A striking similarity was noted between the hypothalami of these two animals. Not only do the nuclei occupy the same position and have the same relations in these two forms, but the cytological structure of the cellular components of homologous nuclei may be considered identical.

In preparation for this study, all of the nuclei and their subdivisions described by Krieg were studied in the brain of the rat, and were then compared with those of the hamster. In the latter animal some of the nuclei are not as easily distinguished. The nucleus preopticus is a rather diffuse group of cell bodies, but has the same position and relations as that of the rat. The nucleus filiformis (paraventricularis of other forms) seems to be more compact and compressed laterally, and more restricted in its extent, with greater intermingling of the partes magnocellularis et parvocellularis. Cytological evidence based on the distribution of Nissl substance along with the shape and density of staining made the division of this nucleus into its two components possible.

The ventromedial complex, composed of five subdivisions, has been identified. Again, as in the former cases, some of the components were separated with difficulty. The partes medialis, centralis, and lateralis are more compressed laterally than in the rat, and are not as individually distinctive. The pars posterior does not exhibit such a strong dorso-lateral and ventro-medial flattening as in the rat.

Krieg employed three planes of section: transverse, frontal, and sagittal. Several staining techniques were employed to determine the course of the fiber connections. In the present paper comparisons of the nuclear patterns of the two forms are based on histological examination of toluidin blue series in transverse section only.

DISCUSSION

Lesions varied in size according to the strength and duration of the administered current and the gauge of the electrode used. Long continuous exposures to electrolytic stimuli resulted in secondary burning up the course of the electrode. Varying degrees of severity of this condition were noted. In some cases secondary burning was negligible and normal cell bodies could be seen adjacent to the electrode path (Figure 11) which, in these instances, was recognizable only by the accumulation of gitter cells. The burning was thought to be due to over-heating of the high resistance nichrome wire used for electrodes rather than to inadequate insulation. Large lesions dorsal to the hypothalamus were used as controls by other authors, and it is apparent from the data that this secondary burning through the thalamic area was not effective in altering the mating response of these animals.

It is believed that the extent of the lesions employed herein cannot be correlated with the mating response since a lesion as small as 0.072 cubic millimeters resulted in refusal to mate and this figure is far below the average for any of the other groups. This lesion, located in the trigone bounded by the nuclei lateralis, ventromedialis pars lateralis, and supraopticus was in what may be considered from the data to be a critical area.

Those animals of Group III (i.e. those animals which refused to mate at the first, or first and second estrus but mated subsequently) very possibly represent a group which reacted temporarily to the operation. Furthermore, it is known that refusal to mate is not uncommon among normal females, and it is possible that initial failure to mate was attributable to the absence of psychic heat despite the manifestation of vaginal heat. If the procedure had been repeated hourly, a positive mating reaction might have been obtained the first night of attempted mating in many of these cases. This conclusion is based on the extensive experience of our laboratories.

The lesions of all animals that refused to mate were situated in the trigone. In all cases, at least a few of the more medial cells of the nucleus lateralis were included in the destruction although the amount of cellular destruction was minor when compared to the great bulk of this nucleus. The nuclei lateralis and ventromedialis pars lateralis are consistently involved in the lesions of animals in Groups I and II because of the juxtaposition of these nuclei. Figure 7 shows the relative position of each. Because of the presence dorsally of the sagittal sinus, no method could be devised to place lesions closer than 1 millimeter from the midline. Destruction of the nucleus ventromedialis without including the more medial portion of the nucleus lateralis was therefore not possible. The nucleus supraopticus was included in the destruction only when the electrode reached the hypothalamic floor.

Because of the consistent position of the lesions in Groups I and II between the three nuclei bounding the trigone, and since relatively few cells are involved, it would appear that the cell bodies of these nuclei could not be responsible for altering the mating responses of these animals. It seems logical, therefore, to assume that an interrupted fiber tract coursing through the ventral portion of the hypothalamus may have been responsible. It may be that the responsible nucleus or nuclei lie anterior to this site and that interrupted efferent pathways to lower levels of the brain stem are responsible for the altered mating responses.

The existence of fiber tracts descending from the hypothalamus and terminating in the reticular substance have been reported in a number of animals. Systematic destruction of small areas of the medulla followed by bipolar stimulation of the hypothalamus altered blood pressure, respiration, and knee jerk reflex in the cat (Thompson and Bach, 1950). Interruption of the medial inhibitory reticular formation in the medulla enhanced hypothalamic facilitation of these responses. Interruption of the dorsolateral facilitative reticular formation resulted in depression or abolition of these responses. Crosby and Woodburne (1951) described descending pathways from the hypothalamus of the macaque monkey. Using the Weil method, they located two pathways which may be of significance in the present work. A posterior hypothalamo-tegmental tract passes from the nucleus ventromedialis and perhaps from the dorsal border of the posterior hypothalamic area. After partial decussation in the supramammillary area it enters the nucleus mesencephalicus profundus. Another pathway, the dorsal hypothalamo-tegmental tract, courses from the ventromedial area to a position dorsal to the red nucleus. This tract also enters the nucleus mesencephalicus profundus pars dorsalis and some of the fibers may enter the interstitial nucleus of the medial longitudinal fasciculus. Morin (1950) showed short fibers from the periventricular system of the guinea pig ending in the nucleus tegmenti profundus.

Brookhart, Dey and Ranson (1941) found that, in ovariectomized guinea pigs with lesions in the anterior hypothalamus, proestrual and estrual behavior could not be induced by injection of ovarian hormones alone or in combination with pituitary hormones. Failure of these animals to mate indicated that efferent fibers emanating from or coursing through the hypothalamus might have been interrupted.

Reference to Figure 1 will reveal that lesions in three animals of Group III (120, 148, and 158), and two in Group IV (122 and 165) were in the general area of the trigone. However, the lesions were in the extreme cephalic or caudal pole of the trigone only. Bilateral lesions in the hypothalamus anterior or posterior to the trigone had no effect in altering the mating response of these animals. These observations indicate that such regions are not directly involved in mediating responses concerned with mating.

During the course of the investigation, several problems for subsequent research have arisen. Electrolytic lesions in the trigone of ovariectomized hamsters should be followed by injection of progesterone into the lateral brain ventricle to ascertain whether or not the results of Kent and Liberman (1949) can be repeated under the new conditions.

Although it is possible that fibers coursing from the hypothalamus to the neocortex may have been affected in the present experiment, rather than those descending in the brain stem, the few experiments concerned with decortication and mating in other animals reduce the probability of such a pathway. However, another investigation should be undertaken to ascertain the origin and termination of fiber tracts interrupted in the present study.

Females with small hypothalamic lesions in this critical area might also be observed for possible alterations in ovulatory cycles, conception, delivery and maternal behavior.

SUMMARY

1. The nuclei of the hypothalamus of the female hamster have been found to be comparable to those of the rat.

2. Electrolytic lesions were placed in various locations in the hypothalamus of 100 mature female golden hamsters. One died as a result of the operation.

3. Bilaterally symmetrical lesions placed in a trigone bounded by the nuclei lateralis, ventromedialis pars lateralis, and supraopticus were effective in abolishing mating activity in the hamster.

4. Lesions placed anterior or posterior to this trigone were ineffective in altering the normal mating responses in these animals.

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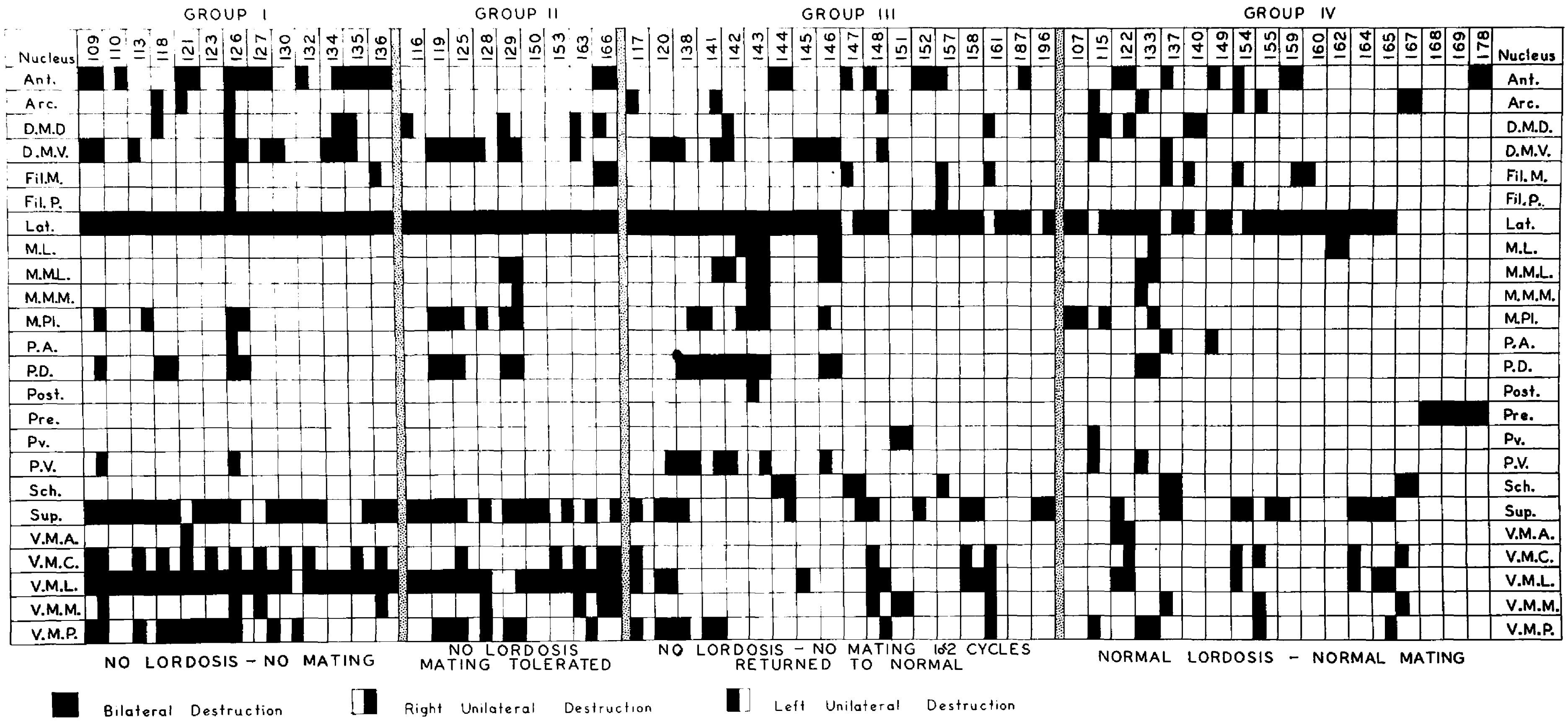
ABBREVIATIONS FOR ALL FIGURES

A.C.	Anterior commissure
Ant.	Nucleus hypothalamicus anterior
Arc.	Nucleus arcuatus
D.M.D.	Nucleus dorsomedialis, pars dorsalis
D.M.V.	Nucleus dorsomedialis, pars ventralis
Fil.M.	Nucleus filiformis magnocellularis
Fil.P.	Nucleus filiformis parvocellularis
Lat.	Nucleus hypothalamicus lateralis
Les.	Electrolytic lesion
M.L.	Nucleus mammillaris, pars lateralis
M.M.L.	Nucleus mammillaris medialis, pars lateralis
M.M.M.	Nucleus mammillaris medialis, pars medialis
M.Pl.	Nucleus mammillaris, pars prelateralis
O.C.	Optic chiasma
O.T.	Optic tract
P.A.	Nucleus periventricularis, anterior division
P.D.	Nucleus premammillaris, pars dorsalis
Post.	Nucleus hypothalamicus posterior
Pre.	Nucleus preopticus
Pv.	Nucleus periventricularis, posterior division
P.V.	Nucleus premammillaris, pars ventralis
Reu.	Nucleus reuniens thalami
Sch.	Nucleus suprachiasmaticus
Sec.B.	Secondary burning
Sup.	Nucleus supraopticus
V.M.A.	Nucleus ventromedialis, pars anterior
V.M.C.	Nucleus ventromedialis, pars centralis
V.M.L.	Nucleus ventromedialis, pars lateralis
V.M.M.	Nucleus ventromedialis, pars medialis
V.M.P.	Nucleus ventromedialis, pars posterior
III	Third ventricle
III P.	Third ventricle, posterior division
III S.M.	Third ventricle, submammillaris division

Figure 1 - Cartograph showing location of electrolytic lesions with respect to nuclear involvement. Note consistent involvement, in Groups I and II, of an area including nuclei lateralis and ventromedialis pars lateralis.

Figure I

SITES OF LESIONS



	GROUP III				GROUP IV														
	111	124	131	175	101	102	103	104	105	106	108	112	139	156	170	171	172	173	174
Ant.			x	x		x		x			x				x	x		x	x
Arc.	x																		
D.M.D.							x		x	x				x					
D.M.V.							x		x	x									
Fil.M.			x			x							x						
Lat.	x			x		x	x	x		x	x		x	x	x	x		x	
M.L.		x																	
M.M.L.					x														
M.M.M.					x														
M.Pl.		x																	
P.A.											x								
P.D.	x								x			x							
Post.		x										x							
Pre.																	x	x	x
P.V.	x								x										
Sch.											x		x						
Sup.						x							x						
V.M.C.			x										x	x					
V.M.L.			x										x	x					
V.M.M.													x						
V.M.P.			x				x		x	x				x					

	GROUP IV																						
	176	177	179	180	181	183	184	186	188	189	190	191	192	193	194	195	197	201	202	205	207	208	
Ant.	x	x	x		x	x	x	x				x	x		x				x	x	x	x	Ant.
Arc.																							Arc.
D.M.D.																							D.M.D.
D.M.V.																							D.M.V.
Fil.M.																							Fil.M.
Lat.	x		x		x	x	x	x			x	x	x										Lat.
M.L.																							M.L.
M.M.L.																							M.M.L.
M.M.M.																							M.M.M.
M.Pl.																							M.Pl.
P.A.																							P.A.
P.D.																							P.D.
Post.																							Post.
Pre.		x		x		x			x	x	x		x	x	x	x	x	x		x	x		Pre.
P.V.																							P.V.
Sch.																			x	x			Sch.
Sup.									x		x												Sup.
V.M.C.																							V.M.C.
V.M.L.																							V.M.L.
V.M.M.																							V.M.M.
V.M.P.																							V.M.P.

Table I - Chart showing location of lesions in forty-one additional animals of Groups III and IV. Nuclear involvement is indicated by "x". No distinction is made between unilateral and bilateral destruction. Those nuclei in which no destruction was noted on either side have been omitted.

Figure 2 - Scale drawings of modifications of the Horsley-Clarke stereotaxic instrument for use on the hamster. X 1

A. Upper head plate

B. Lower head plate (vertical columns removed)

C. Lower head plate (rear view)

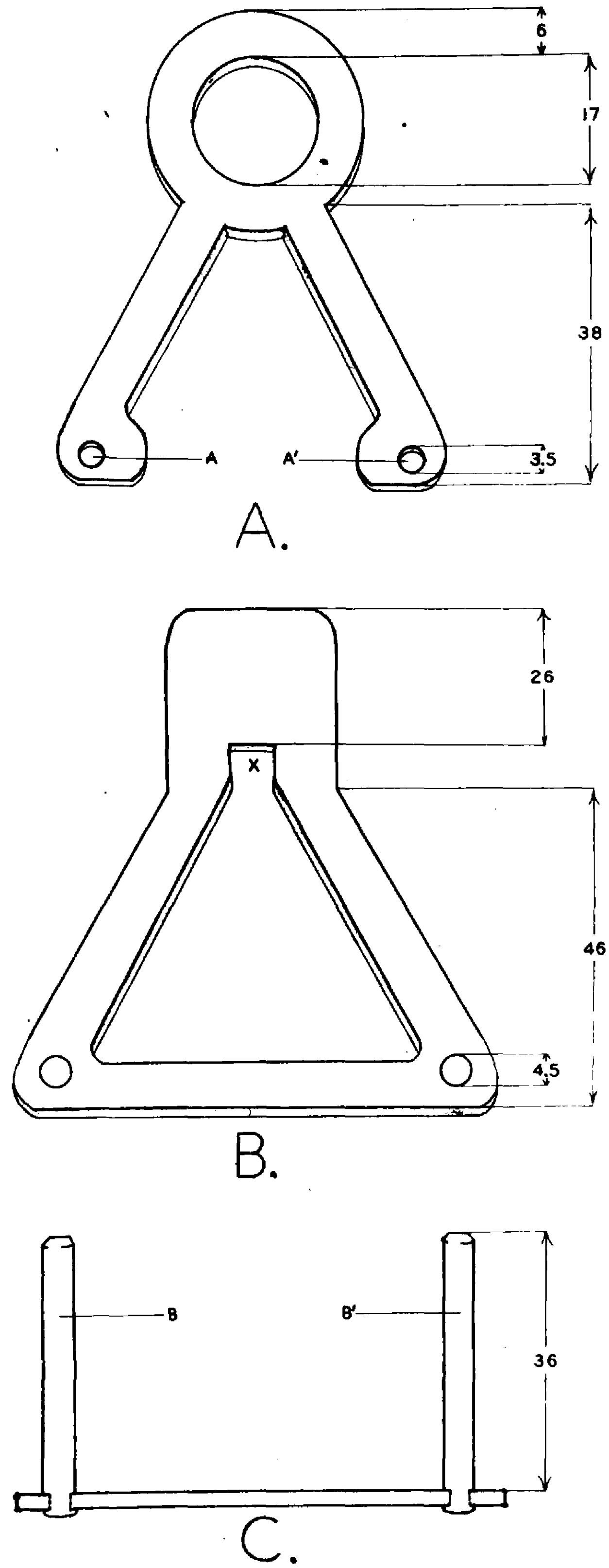


Figure - 2

MODIFICATIONS FOR THE HORSLEY-CLARKE INSTRUMENT

Figure 3 - Cross section of the ventral portion of the diencephalon through the preoptic region. X 20

Figure 4 - Cross section through the anterior portion of the hypothalamus showing relative positions of hypothalamic nuclei of the intact animal. X 20

Figure 5 - Cross section of the hypothalamus of an intact animal at a more caudal level showing location of nuclei. X 20

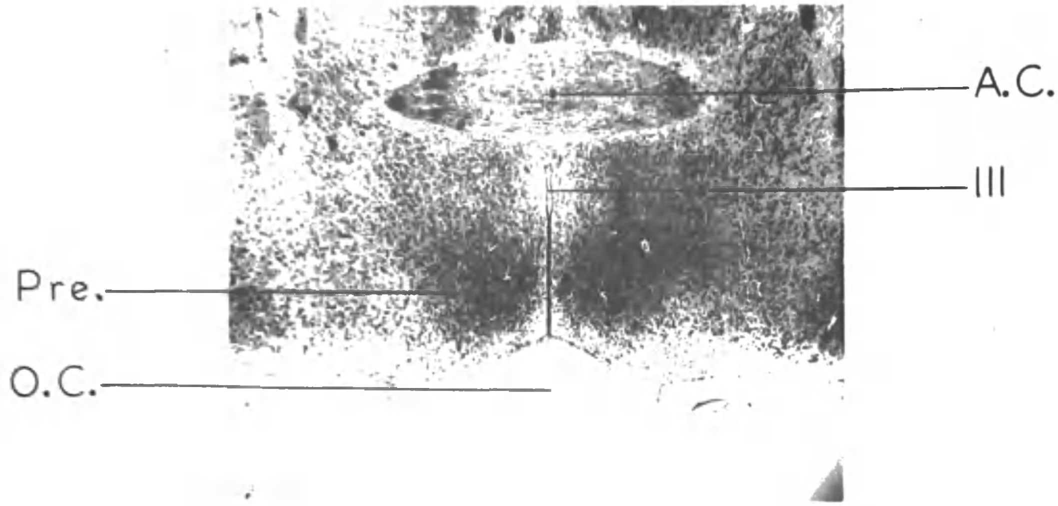


Figure 3

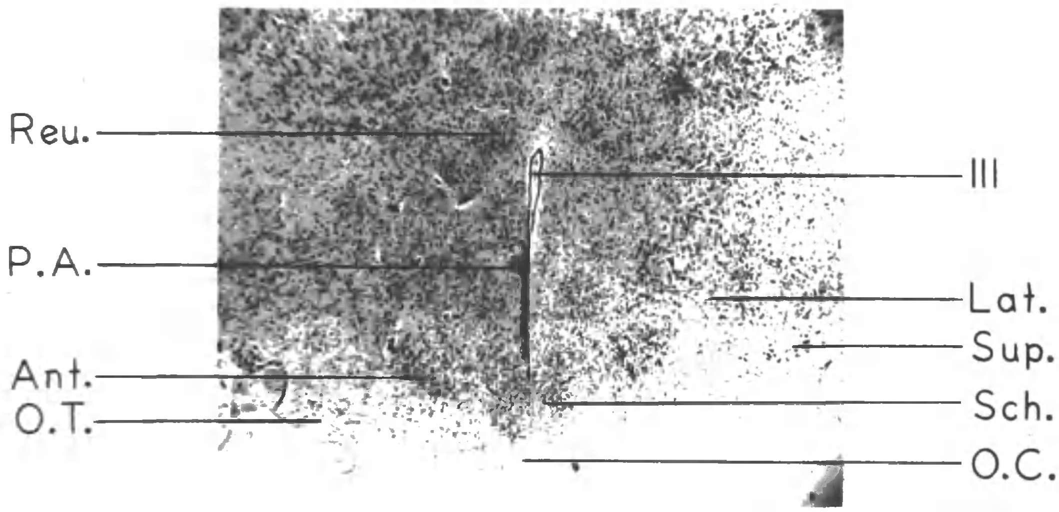


Figure 4

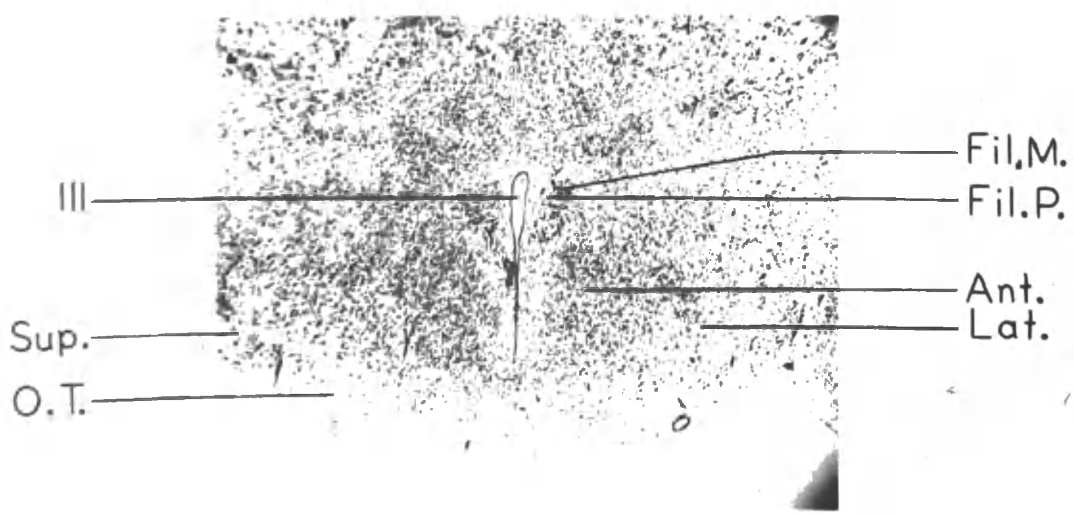


Figure 5

Figure 6 - Cross section of the hypothalamus at the level of the cephalic pole of the ventromedial complex (V.M.A.). The nucleus supraopticus now occupies a position at the hypothalamic floor. X 20

Figure 7 - Cross section of the hypothalamus at the level of the trigone (Lat., V.M.L., and Sup.). X 20

Figure 8 - Cross section of the caudal hypothalamus through the mammillary and premammillary areas. X 20

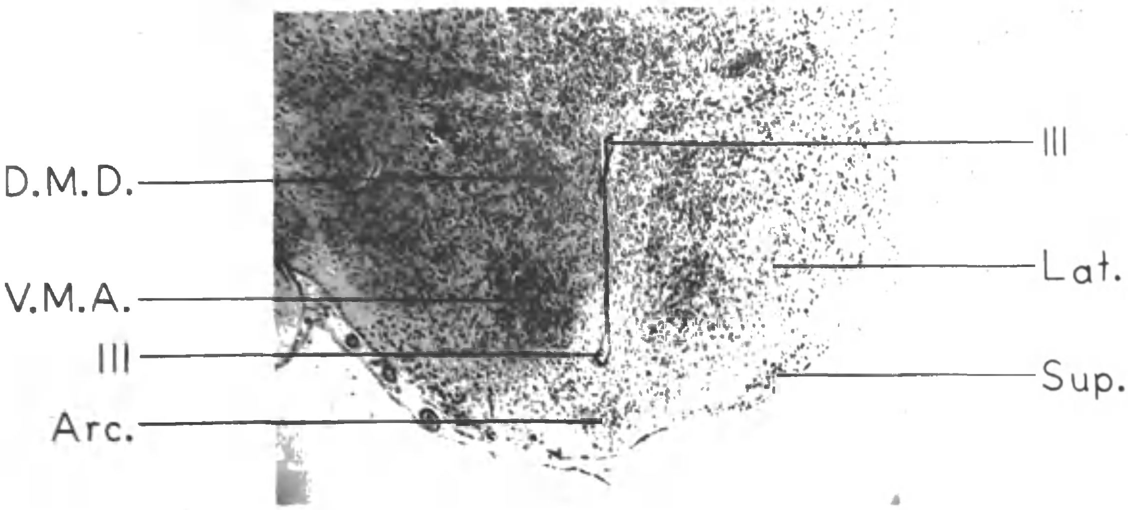


Figure 6

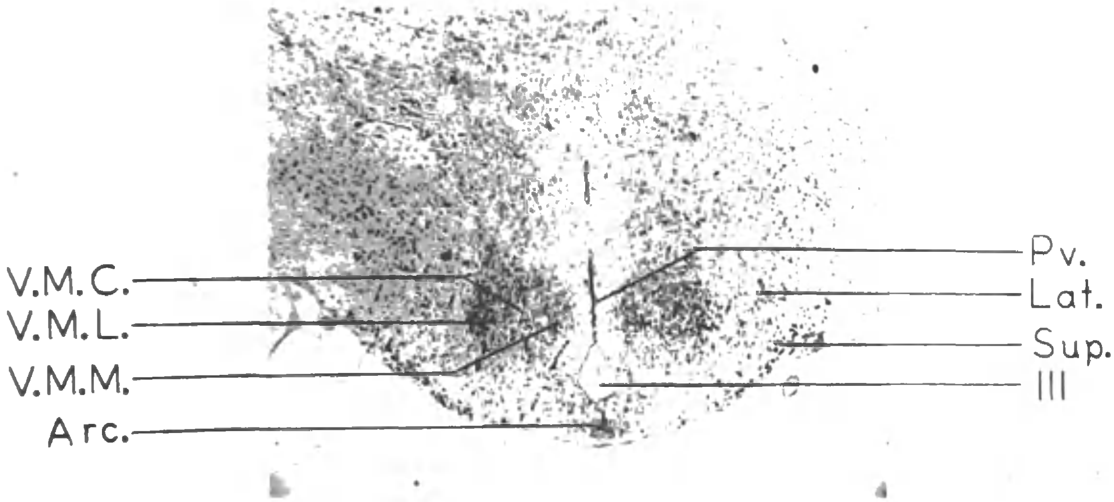


Figure 7

Figure 8

Figure 9 - Cross section of the hypothalamus at the level of the trigone showing critically placed lesions. Note destruction of the nucleus supraopticus on the left side only. For positions of nuclei of the trigone see Figure 7. X 20

Figure 10 - Cross section of the hypothalamus at the level of the trigone. Symmetrically bilateral lesions involved the three nuclei bounding the trigone on either side. X 20

Figure 11 - Cross section of the hypothalamus at the level of the trigone showing asymmetrically bilateral lesions. The right lesion was critically placed in the area of the trigone. X 20

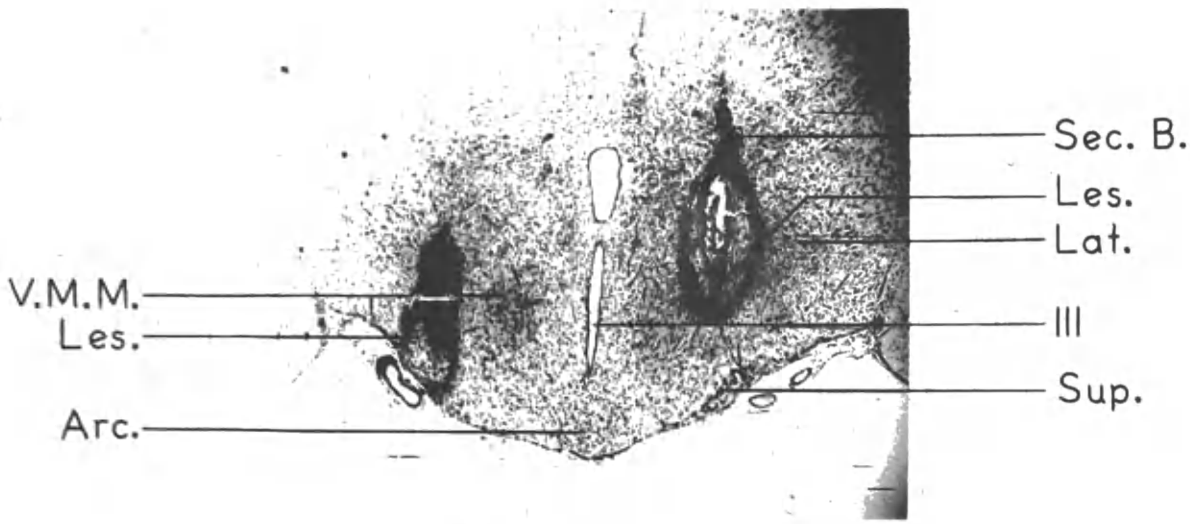


Figure 9

Figure 10

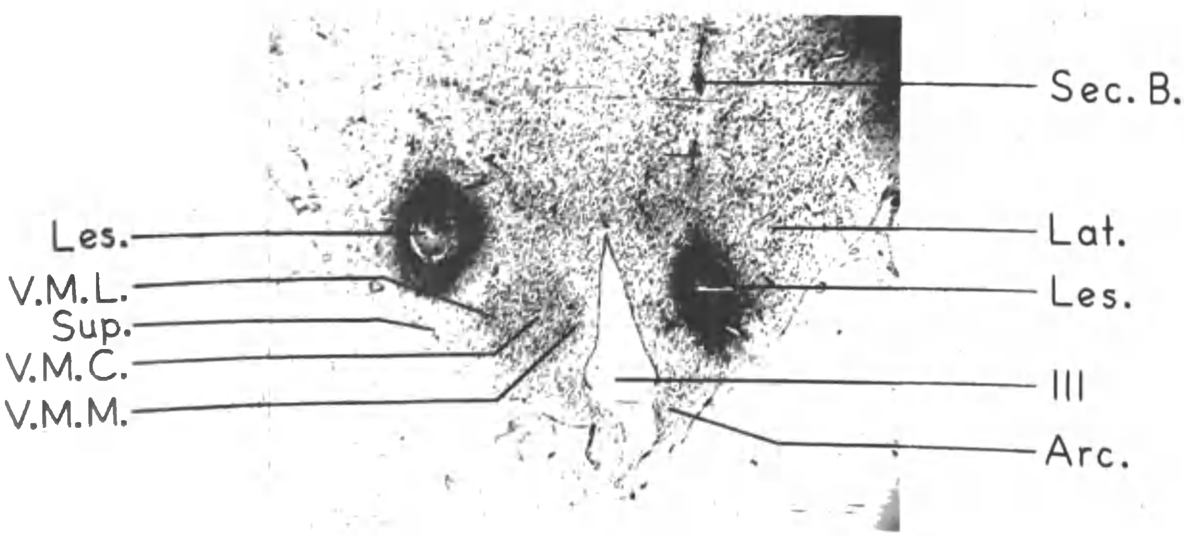


Figure 11

Figure 12 - Cross section of the anterior hypothalamus showing small symmetrically bilateral lesions. For positions of the nuclei, see Figure 4. X 20

Figure 13 - Cross section of the posterior hypothalamus showing symmetrically bilateral lesions. For positions of the nuclei involved in the destruction, see Figure 8. X 20

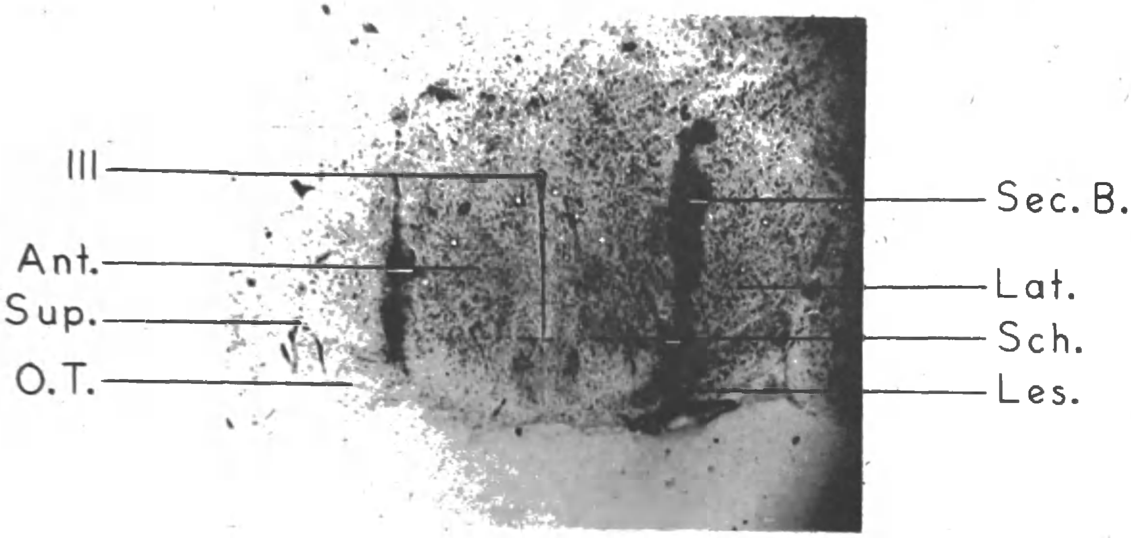


Figure 12

Figure 13

BIOGRAPHY

George Van Sickel White was born in Opelousas, Louisiana on December 15, 1923. He attended public schools in Port Barre, Louisiana and completed his high school work at Opelousas High School in 1940. He attended Southwestern Louisiana Institute from 1940 to 1944 at which time he received a Bachelor of Science degree. Between 1944 and 1946 he served in the Army of the United States from which he was honorably discharged. He entered the Graduate School at Louisiana State University in 1946 and received the degree of Master of Science in 1947. From 1950 to 1953 he was a member of the faculty at Westminster College in Fulton, Missouri. He returned to Louisiana State University in 1953 and completed the requirements for the degree of Doctor of Philosophy in 1954.

EXAMINATION AND THESIS REPORT

Candidate: George V. S. White

Major Field: Zoology

Title of Thesis: Certain effects of electrolytic lesions in the hypothalamus on the mating behavior of the golden hamster

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

May 7, 1954